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2021-01

Singh , J , Cameron , E , Reitz , T , Schädler , M & Eisenhauer , N 2021 , ' Grassland management effects on earthworm communities under ambient and future climatic conditions ' , European Journal of Soil Science , vol. 72 , no. 1 , pp. 343-355 . https://doi.org/10.1111/ejss.12942

http://hdl.handle.net/10138/333656
https://doi.org/10.1111/ejss.12942

Received: 11 September 2019 | Revised: 26 January 2020 | Accepted: 4 February 2020

DOI: 10.1111/ejss.12942

ORIGINAL ARTICLE

European Journal of Soil Science WILEY

Grassland management effects on earthworm communities under ambient and future climatic conditions

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Funding information
Academy of Finland, Grant/Award Number: 285882; Alexander von Humboldt-Stiftung, Grant/Award Number: 3.5/INI/1164712; Deutsche Forschungsgemeinschaft, Grant/Award Number: FZT 118; Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: RGPIN-2019-05758

Abstract

The impacts of climate change on biodiversity can be modulated by other changing environmental conditions (e.g. induced by land-use change). The potential interactive effects of climate change and land use have rarely been studied for soil organisms. To test the effects of changing climatic conditions and land use on soil invertebrates, we examined earthworm communities across different seasons in different grassland-use types (intensively managed grassland, extensively managed meadow and extensively managed sheep pasture). We predicted that the strength of climate change effects would vary with season and land use. Overall, extracted earthworm populations showed the strongest variations in response to the season, indicating major differences in activity patterns and extraction efficiency, whereas climate change and different grassland-use types had fewer and weaker effects. Future climate, characterized by slightly higher precipitation in spring and autumn but a strong reduction during the summer, had positive effects on the abundance of extracted adult earthworms in spring but then reduced the abundance of active earthworms across the remaining seasons. In contrast, the total biomass of juveniles tended to be consistently lower under future climate conditions. Earthworm species responded differently to the climate change and different grassland management types, and these species-specific responses further varied strongly across seasons. Intensive grassland management had negative effects, due to plant community composition, whereas sheep grazing favoured earthworm populations, due to dung deposition. There were only limited

interactive effects between climate and land use, which thus did not support our main hypothesis. Nevertheless, these results highlight the complex and context-dependent responses of earthworm communities and activity patterns to climate change, with potential consequences for long-term population dynamics and crucial ecosystem functions.

Highlights

- We explored earthworm communities in response to climate change, different grassland-use types and seasons
- Climate had species-specific effects on active earthworms, but few interactions with land-use type
- Intensive grassland management decreased, but sheep grazing favoured, active earthworm populations
- Strong seasonal variations in earthworm activity periods will be modulated by climate change

KEYWORDS

climate change, drought, earthworms, ecosystem engineers, land use types, land-use intensity, soil biodiversity, warming

1 | INTRODUCTION

Ecological communities are increasingly threatened by global environmental changes, including climate change (Tylianakis et al., 2008) and land-use change (Newbold et al., 2015). These changes can impact organisms directly by affecting their activity and mortality, and indirectly through effects on interacting taxa (Bardgett, Manning, Morrien, & De Vries, 2013). Interactions between global environmental change agents can also occur (e.g., Kardol, Cregger, Campagny, & Classen, 2010; Thakur et al., 2018), such that the direction and magnitude of effects of one stressor are influenced by another stressor. Predicting the effects of multiple stressors is challenging as the combined effects of two stressors may be additive, synergistic (combined effects are greater than the sum of effects from individual stressors) or antagonistic (less than the sum of individual effects) (Cote, Darling, & Brown, 2016).

Soil biodiversity supports a wide range of ecosystem processes and services, including nutrient cycling, water purification and crop production (Wall, Bardgett, Behan-Pelletier, Herrick, & Jones, 2013), and influences how soil ecosystems respond to human-induced changes in climate and land use (Kardol et al., 2010; Yin et al., 2019). Among soil organisms, soil macro-detritivores like earthworms are key drivers of ecosystem functions, such as litter decomposition, carbon flux and the maintenance of soil structure (Lavelle, 1997), and are increasingly used as an indicator group in soil quality assessments (Fründ, Graefe, & Tischer, 2011). Earthworms are likely to be strongly impacted by global change because their abundance and biomass are determined by the presence of sufficiently high levels of soil moisture (Hackenberger & Hackenberger, 2014; Perreault & Whalen, 2006; Singh, Schädler, Demetrio, Brown, & Eisenhauer, 2019) and the availability and quality of organic matter as a food resource (Abbott & Parker, 1981; Amosse, Turberg, Kohler-Milleret, Gobat, & Le Bayon, 2015; Lüscher et al., 2015).Various climate change drivers, such as increasing temperature, may elevate metabolic demands and affect the life cycle and nutrition of soil animals as well as water availability in the soil (Thakur et al., 2018). Increases in the frequency of extreme precipitation events and droughts (Bates, Kundzewicz, Wu, & Palutikof, 2008) may additionally cause mortality. Moreover, elevated frequency and intensity of extreme rainfall and changes in land use may make soils more vulnerable to degradation and erosion (Nearing, Pruski, & O'Neal, 2004) and thus affect earthworm distributions.

Grasslands cover 40% of the earth's land surface and are of high economic, ecological and biodiversity value due to their role in providing forage for livestock and retaining high levels of carbon in the soil (Lee, Manning, Walker, & Power, 2014; Lenhart, Eubanks, & Behmer, 2015). Invertebrates are the main component of faunal diversity in grasslands, playing substantial roles in ecosystem processes, including nutrient cycling and pollination. As compared to other habitats in temperate ecosystems, earthworms are generally more abundant and diverse in grasslands (Rutgers et al., 2009; Keith, Boots, Stromberger, & Schmidt, 2018; Spurgeon, Keith, Schmidt, Lammertsma, & Faber, 2013),

particularly in areas with higher organic matter content and nitrogen mineralization rates (van Vliet, van der Stelt, Rietberg, & de Goede, 2007). But grasslands have been dramatically transformed over time due to intensification of agricultural practices and consequent loss of plant diversity (Buttler et al., 2012; Manning et al., 2015). Land-use change is one of the primary drivers of biogeochemical change in modern agroecosystems, and its intensification can affect earthworm diversity (Postma-Blaauw, de Goede, Bloem, Faber, & Brussaard, 2012; Tao et al., 2013) and have significant effects on soil fertility, water infiltration and soil erosion (Paoletti, 1999). Furthermore, plant communities in grasslands are also being altered by climate change, and disturbance regimes are changing under the combined effects of climate change, biological invasions and direct human modifications of the environment (Mandal & Neenu, 2012).The resulting changes in plant community diversity and composition have been shown to influence the diversity and activity of earthworms and other soil biota (e.g. Eisenhauer et al., 2009; Sabais, Scheu, & Eisenhauer, 2011).Thus, ecological communities in grassland soils and associated functions are likely to be affected by multiple co-occurring, and potentially interacting, global change drivers (Eisenhauer et al., 2012a, 2012b).

The impacts of climate change and land-use change on earthworms may vary depending on their habitat preferences. Epigeic species living at the soil surface are likely to be strongly affected by successive dry summers. Endogeic earthworms, which make horizontal burrows in the top ~30 cm of the soil, have been shown to be very sensitive to drought conditions (Jiménez & Decaëns, 2004; Jouquet et al., 2007; McDaniel, Stromberger, Barbarick, & Cranshaw, 2013), although they are able to survive for short periods of drought by forming aestivation chambers composed of mucus and gut content to protect against water loss (Eggleton, Inward, Smith, Jones, & Sherlock, 2009; Bayley et al., 2010; McDaniel et al., 2013). Anecic earthworms that form permanent vertical burrows in soil can enter diapause during a dry period and stay a few months in a dormant stage (Jiménez & Decaëns, 2004) and thus may be less sensitive to drought conditions. Given these differences in life-history traits among earthworm ecological groups and species, climate change may alter the composition and activity patterns of earthworm communities and thus subsequent ecosystem effects.

Although climate change and land-use change are known to represent major threats to biodiversity (Díaz et al., 2019; Sala et al., 2000), there are still few studies investigating climate-change effects under multiple land-use scenarios, including a range of management and cultivation measures. Furthermore, studies have rarely examined how the interactive effects of global change drivers influence soil communities and how these effects may vary over time (Eisenhauer et al., 2018; Siebert et al., 2019a). For instance, effects of reduced precipitation on earthworm communities and their activity may be stronger during dry and warm summer months compared to wet and colder spring and autumn months (Siebert et al., 2019b; Thakur et al., 2018).

Here, we tested the effects of changing climate conditions and different grassland-use types on earthworm populations across seasons. Specifically, we predicted that: (a) climate change will decrease active earthworm densities and populations; (b) the strength of climate change effects will depend on grassland management, with the most detrimental effects occurring under intensive land use; and (c) environmental change effects will depend on the season, with strongest detrimental effects during the summer months with reduced precipitation and intensive land use, and less negative effects in spring and autumn. These detrimental effects of climate may be more pronounced for endogeic earthworms as compared to anecic earthworms, whereas endogeic earthworms may be less affected by land use than anecic earthworms.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental treatments

Our study was conducted within the Global Change Experimental Facility (GCEF) at Bad Lauchstädt, Halle, Saxony-Anhalt, Germany (51° 22′ 60 N, 11° 50′ 60 E).The study site is characterized by low mean annual precipitation (484 mm) and a mean temperature of 8.9°C (long-term means 1896–2013) and has a high content of humus down to a depth of more than 40 cm (Altermann et al., 2005; Schädler et al., 2019). The soil is a Haplic Chernozem, which is highly fertile and typically developed upon carbonatic loess substrate under summer dry climatic conditions (Altermann et al., 2005).

The GCEF is an experimental platform designed to investigate the consequences of climate change on species, communities and ecosystem functions in different land-use types (see further details in Schädler et al., 2019). We examined earthworm communities in plots belonging to three of the five land-use types included in the GCEF: (a) intensively managed grassland (IM), (b) extensively managed meadow (EM) and (c) extensively managed sheep pasture (EP). In the GCEF, there are 50 experimental plots; 30 of those are grassland plots (16 m × 24 m), which are arranged into 10 groups of three plots each. Half of the groups of plots were assigned to ambient climate and the other half were subjected to a future climate scenario. This resulted in a split-plot design with climate as the main-plot factor and land use as the subplot factor (five replicates

per climate × land use combination), with a minimum distance of 25 m between the main plots.

The future climate treatment was based on a consensus scenario for central Germany for the period 2070–2100 across 12 climate simulations, under four different emission scenarios with three established regional climate models: COSMO-CLM (Rockel, Will, & Hense, 2008), REMO (Jacob & Podzun, 1997) and RCAO (Döscher et al., 2002). According to these scenarios, mean temperature is predicted to increase by ~2°C, whereas precipitation is expected to decrease by ~20% during the summer months, but to increase by ~10% during spring and autumn. In the GCEF, mobile roofs and side panels are used to increase night temperatures in periods without strong frosts, which resulted in an increase of the daily mean of air temperature close to the ground (5 cm height) by +0.55% during the roof phase. The daily mean soil temperature at a depth of 0 cm to −10 cm was increased by +0.62°C, and by +0.50°C at a depth of −15 cm to −25 cm.

The roofs in combination with an irrigation system (using rainwater) are further used to manipulate the precipitation pattern. After heavy rain events in spring and autumn, we added ~10% of ambient rain via the irrigation system to the subplots with future climate. In summer, a rain sensor controlling the roofs together with the irrigation system was used to adjust precipitation on the future climate subplots to ~80% of ambient rainfall. The manipulation of temperature and precipitation started in April and July 2014, respectively.

The intensively used grasslands were established by sowing in summer/autumn 2014 from a commercially available seed mixture, which is recommended for the study region and consists of five grass species/cultivars. In the extensively used meadows, we established species-rich grasslands in spring/summer 2014 from the regional species pool, including 14 grass species, 10 legumes and 32 other herbs, which are typical for mesotrophic and mesophilous to dry meadows and pastures as well as steppe grasslands of the region (see further details on species and sowing densities in Schädler et al., 2019).The intensively used grassland was managed by four cuts per year followed by moderate fertilization. The extensively used meadow was managed by two cuts and no fertilization (see Schädler et al., 2019 for details). The extensively used pasture was managed by one (2015) or two (2016) short-time high-intensity grazing events (20 sheep for 24-hr per subplot).

2.2 | Earthworm sampling

To examine potential changes in active earthworm populations over time, earthworm surveys were conducted during the last weeks of April, June, August and October 2017. Samples were taken along a transect of 15 m across the plots, excluding a buffer zone of 4.5 m to each of the open sides of the plots, which are not closed by panels during the night to avoid edge effects. The distance between the samples taken at different time-points on the same plot was 50 cm. One sample per plot and time-point was taken, giving a total of 130 samples. The upper 10 cm of soil within a 50 cm × 50 cm metal frame was excavated, and soil was hand-sorted for earthworms. Afterwards, the resulting pits were used for additional mustard extraction of earthworms. Mustard water was prepared the night before sampling by dissolving 100 g of mustard powder in 5 L of water (Eisenhauer, Straube, & Scheu, 2008). An additional 5 L of water was mixed into the solution prior to sampling. To extract earthworms, 5 L of mustard solution was poured into the excavated frame and earthworms were collected into a container as they emerged from the soil. After 15 min, the remaining 5 L of mustard solution was added and earthworms were collected for a total of 30 min. Earthworms were counted, weighed and stored in 70% ethanol in the laboratory. Earthworms were identified to species level (except juveniles) by using taxonomic keys (Gates, 1972; Sims & Gerard, 1999). Earthworm extraction efficiency was shown to differ according to soil moisture conditions (e.g., Eisenhauer et al., 2008), with substantial variations in ecological group-specific earthworm activity patterns across seasons (e.g., Eisenhauer et al., 2014). Thus, the reader should note that we present data on active earthworm densities and biomass during these extraction events, but that actual changes in population sizes may be less pronounced.

2.3 | Analyses of soil moisture and soil pH

For the analysis of soil moisture, seven soil cores (1 cm diameter, 15 cm deep) were taken along a 15-m transect in each plot, pooled and sieved at 2 mm at 10 dates in 2017. Gravimetric soil moisture contents were determined using a fully automatic moisture analyser (Kern DBS60-3, Kern & Sohn GmbH, Ziegelei 1, Balingen-Germany). pH values were assessed at the end of August 2017 using 20 soil cores (12 mm diameter, 30 cm deep), which were separated into two depth levels (0–15 cm and 15–30 cm). Cores of each depth level were pooled and sieved at 2 mm. pH was measured from air-dried soil with a pH electrode (Mettler Toledo InLab Expert Pro-ISM, Mettler-Toledo GmbH Ockerweg 3, Giessen, Germany) after shaking soil for 1 hr in 0.01 M $CaCl_2$ (1:2.5 w/v).

2.4 | Statistical analyses

We analysed the effects of climate change, grassland-use type and sampling date on species richness, total and individual biomass, and abundance of active earthworms using repeated measures generalized linear mixed split-plot models (SAS v 9.4). Juvenile earthworms could not be identified to the species level, and thus only total biomass and total individual numbers were analysed. For adult earthworms, analyses of biomass and abundance were further conducted at the species level. Biomass data were log-transformed prior to analyses to meet the requirements of parametric statistical tests. Count data (species richness, individual numbers) were analysed assuming Poisson-distributed residuals with a log-link function. In a few cases, there was indication of over-dispersion according to generalized chi-squared/*df* ratios, and therefore we assumed negative binomial-distributed residuals. The superior fit of the selected distributions was further confirmed using the Akaike Information Criterion. The proportion of juveniles was analysed as a binary response variable using a generalized linear mixed model with repeated measurements with logit link function. All analyses yielding significant results were followed by Tukey's post-hoc tests.

3 | RESULTS

3.1 | Earthworm abundance and biomass

Four endogeic earthworm species (*Octolasion cyaneum, Allolobophora chlorotica, Aporrectodea rosea* and *Aporrectodea caliginosa*) and one anecic species (*Lumbricus terrestris*) occurred in the three grassland types. In total, ~24% of the earthworms extracted were adults and ~76% were juveniles. Adults made up ~58% of the total earthworm biomass. *Lumbricus terrestris* had the highest biomass (~48% of adult biomass), whereas *A. rosea* was the most common species sampled (~32% of the total adult earthworm population) (Table S1).

3.2 | Climate change and land-use effects on earthworm communities

Earthworm abundance was most strongly affected by sampling date (season), with the abundance of both adults and juveniles being lowest in June (early summer) and highest in October (autumn) (Figure 1). However, the climate and land-use treatments also interacted with the season to influence earthworm abundance (Tables 1 and 2). Specifically, adult earthworms tended to be more abundant under future climate conditions than under ambient climate conditions in spring (+ 41%), whereas they tended to have lower abundances in the future climate treatment in late summer (−30%) and autumn (−29%, Figure 1a). In contrast, the abundance of juveniles did not vary significantly in relation to climate conditions, but it differed across grassland types over time (significant land use × season interaction, see Table 1). Abundance of juveniles was lowest in early summer and highest in autumn. The increase in abundance at the end of the season was weaker in the intensively used grasslands (Figure 1b).The number of earthworm species and Shannon evenness of adult earthworms were not significantly affected by climate or land use (all $p > .05$) but differed among

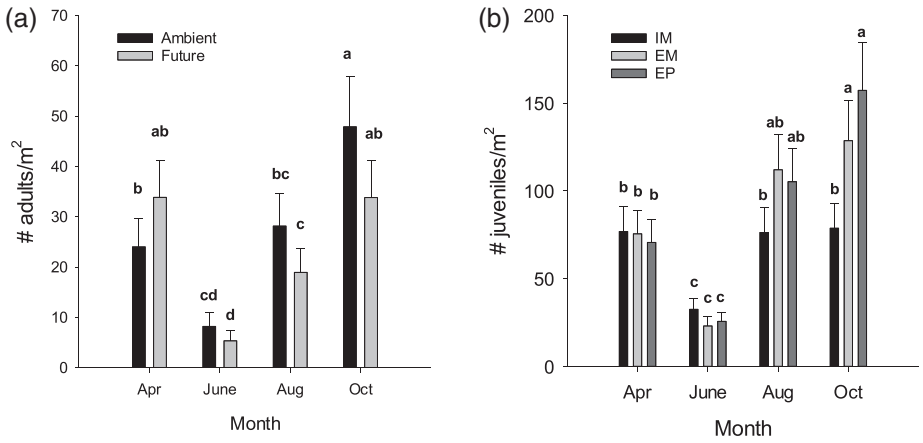

FIGURE 1 Earthworms as affected by climate change, grassland type and season. (a) Abundance of adult earthworms as affected by climate (ambient vs. future) and season (April = spring, June = early summer, august = late summer, October = autumn). (b) Abundance of juvenile earthworm distribution as affected by land use (intensively used meadow, extensively used meadow and extensively used pasture) and season. Means with standard error. Different letters indicate significantly different means following Tukey's post-hoc test ($p < .05$). EM, extensively used meadow; EP, extensively used pasture; IM, intensively used meadow

TABLE 1 Generalized linear model results for the abundance of earthworms as affected by climate (C; ambient vs. future), land use (L; intensively used meadow, extensively used meadow and extensively used pasture), season (S; spring, early summer, late summer, autumn) and all possible interactions. Given are *F*-values and significance levels as * = $p < .05$, ** = $p < .01$ and *** = $p < .001$

	Climate	Land use	Season	C × L	C × S	L × S	C × L × S
df	**1.8**	**2.16**	**3.24**	**2.16**	**3.24**	**6.48**	**6.48**
Total	1.82	0.67	34.21***	1.27	0.74	1.70	0.96
Adults	0.48	2.06	23.32***	1.35	3.10*	0.41	0.67
Juveniles	2.45	0.54	46.15***	0.76	0.70	2.40*	2.02
Lumbricus terrestris	1.18	3.11	6.79***	1.37	1.76	0.25	1.43
Octolasion cyaneum	1.45	2.49	7.91***	0.29	0.20	1.05	1.04
Allolobophora chlorotica	1.34	1.50	2.81	1.70	1.37	0.98	1.24
Aporrectodea rosea	1.01	1.58	4.97**	2.23	3.05	0.46	0.49
Aporrectodea caliginosa	0.24	0.67	4.18*	0.54	0.96	0.68	1.32

TABLE 2 Generalized linear model results for the biomass of earthworms as affected by climate (C; ambient vs. future), land use (L; intensively used meadow, extensively used meadow and extensively used pasture), season (S; spring, early summer, late summer, autumn) and all possible interactions. Given are *F*-values and significance levels as * = $p < .05$, ** = $p < .01$ and *** = $p < .001$

	Climate	Land use	Season	C × L	C × S	L × S	C × L × S
df	**1.8**	**2.16**	**3.24**	**2.16**	**3.24**	**6.48**	**6.48**
Total	<0.01	5.90**	54.50***	1.56	0.83	0.27	0.61
Adults	1.28	5.47**	26.64***	0.55	1.22	0.17	0.74
Juveniles	4.85	3.34	105.36***	4.40*	2.52	1.99	2.36*
Lumbricus terrestris	4.25	1.77	3.70*	0.40	3.78*	0.44	0.90
Octolasion cyaneum	<0.01	6.84**	29.35***	0.29	0.34	1.26	0.97
Allolobophora chlorotica	1.42	4.51*	1.12	4.80*	0.02	0.51	0.50
Aporrectodea rosea	1.58	3.12	12.34***	2.05	3.83*	0.65	0.73
Aporrectodea caliginosa	0.53	0.71	4.79**	0.42	1.32	0.64	0.44

dates with the lowest values in early summer (June) (mean species richness: April, 2.50; June, 1.47; August, 2.23; October, 2.70 ± 0.15 common standard error; evenness (mean + standard error): April, 0.76 ± 0.07; June, 0.40 ± 0.08; August, 0.63 ± 0.07; October, 0.71 ± 0.08; all $p < .05$). Further, the proportion of juvenile earthworms was not affected by climate, land use or season (all $p > .05$).

Earthworm biomass across all species was also most strongly affected by sampling date and was lowest in June. Land use had significant effects on total biomass, adult biomass and juvenile biomass, with the intensively managed meadows having lower biomass than the extensively managed meadows and pastures (Figure 2a). The highest biomass values could be found for the extensive pastures (compared to intensively used meadows: +64% for total biomass, +59% for adult biomass and +72% for juvenile biomass). Similarly, the intensively managed meadows also had the lowest mean biomass of individuals (+25% for extensive meadows and +43% for extensive pastures, Figure 2b). Climate, land use and season interacted to impact juvenile biomass. Specifically, the total biomass of juveniles tended to be consistently lower under future climate conditions; this difference was significant for extensively used meadows in June (early summer, −81%), August (late summer, −34%) and October (autumn, −22%) (Figure 2c).

The species-specific abundances of earthworms showed no significant responses to main effects of climate or land use, but were affected by season and interaction effects of season and climate as well as land use and climate. The interaction between season and climate conditions had significant effects on the total biomass of *L. terrestris*, with a higher biomass present in the future climate treatment, especially in August, but a trend towards lower values in October (Figure 3a). In contrast, *A. rosea* showed a significantly higher total biomass under future conditions only in spring (April). The total biomass of *Allolobophora chlorotica* depended on a significant land use × climate interaction with a very low

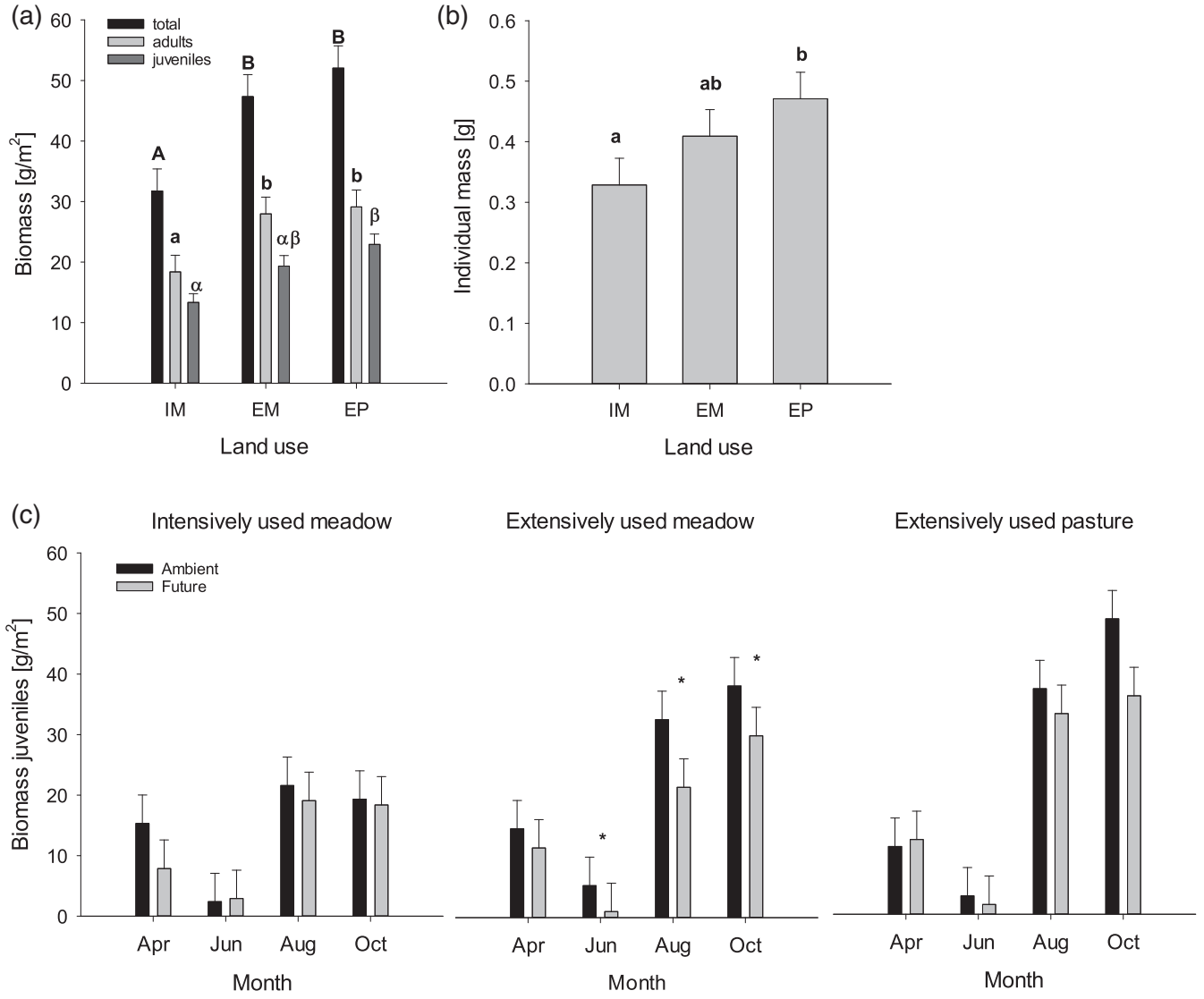

FIGURE 2 Earthworms as affected by climate change, grassland type and season. (a) Biomass of total, adult and juvenile earthworms as affected by climate (ambient vs. future) and grassland type (intensively used meadow, extensively used meadow and extensively used pasture). Different letters indicate significant differences following Tukey's post-hoc test ($p < .05$). Upper case, lower case and Greek letters refer to separate analyses of age classes. (b) Individual biomass of earthworms as affected by climate and grassland type. Different letters indicate significant differences following Tukey's post-hoc test ($p < .05$). (c) Biomass of juvenile earthworms as affected by interacting effects of climate, land use and season (April = spring, June = early summer, August = late summer, October = autumn). Asterisks indicate significant differences of means between climate treatments within a given land use × season combination following Tukey's post-hoc test ($p < .05$). EM, extensively used meadow; EP, extensively used pasture; IM, intensively used meadow

biomass in the intensively used meadows under both climatic conditions and in the extensively used meadow only under future climatic conditions, but high biomass under ambient climate conditions (Table 2, Figure 3c).

Only three species were common enough to allow an analysis of the mean biomass per individual. Although the individual biomass of *A. rosea* and *L. terrestris* was not affected by any of the treatments (all $p > .05$), the mean individual biomass of *O. cyaneum* was affected by an interactive effect between all three experimental factors: future climate had a positive effect on the mean individual biomass of *O. cyaneum* in the intensively used grassland and extensively used grassland in spring (only April), whereas no significant effect was observed in the extensively used pasture (Figure 3d, Table S2).

3.3 | Effects on soil moisture and pH

Climate change generally decreased soil moisture across the year ($p < .05$). This effect interacted with sampling date and was not detectable in summer when the soil was generally very dry (Figure S3a, climate × sampling date interaction: $p < .05$). At the end of spring, the effect

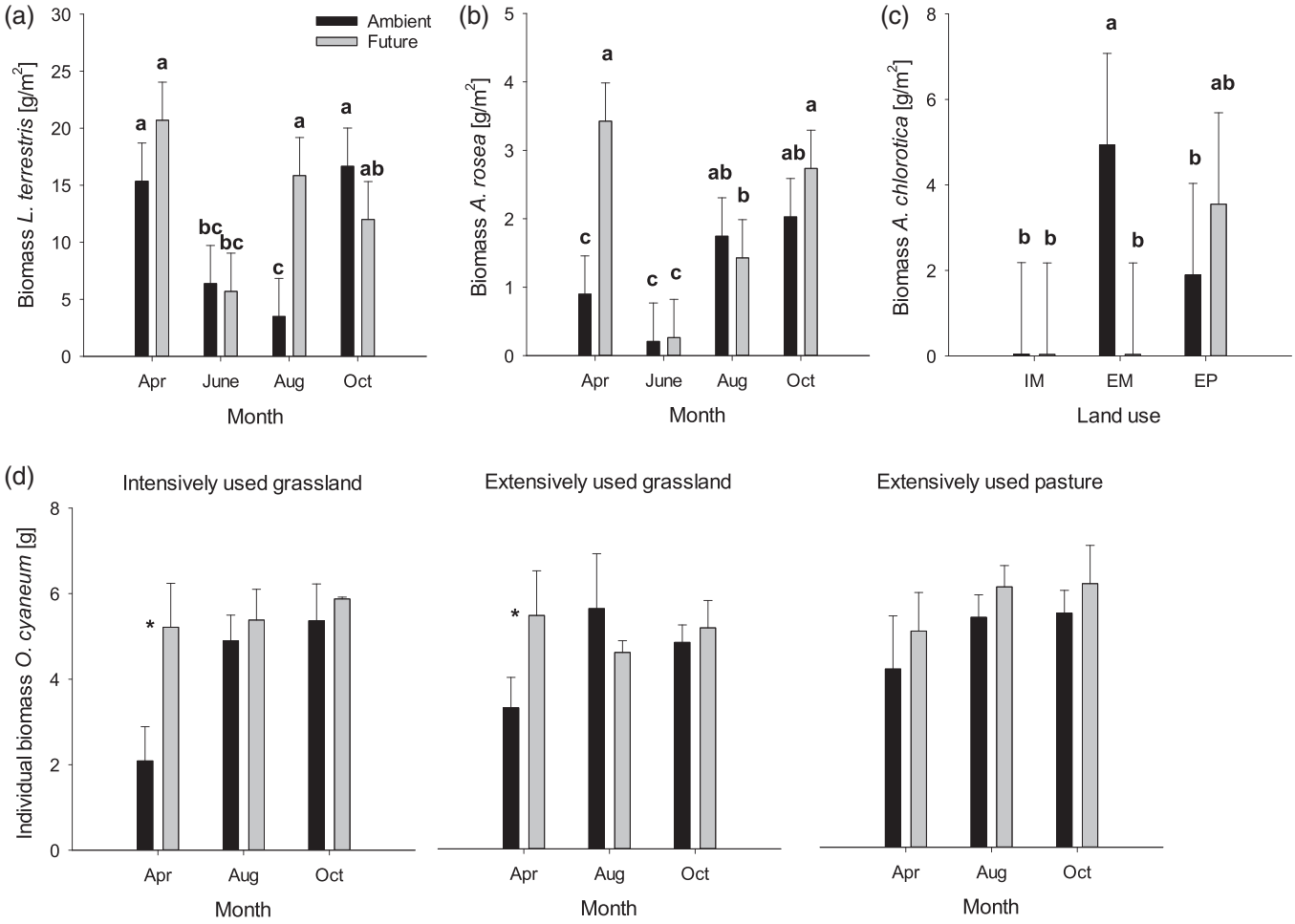

FIGURE 3 Earthworms as affected by climate change, grassland type and sampling date. (a) Biomass of *Lumbricus terrestris* as affected by climate (ambient vs. future) and season (spring = April, early summer = June, late summer = August, autumn = October); (b) biomass of *Allolobophora rosea* as affected by climate and season; and (c) biomass of *Allolobophora chlorotica* as affected by climate and grassland type (intensively used meadow, extensively used meadow and extensively used pasture). Different letters indicate significant differences between means following Tukey's post-hoc test ($p < .05$). (d) Interacting effects of climate, grassland type and sampling date on individual biomass of *Octolasion cyaneum*. Asterisks indicate significant differences of means between climate treatments for given land use × season combinations following Tukey's post-hoc test ($p < .05$). EM, extensively used meadow; EP, extensively used pasture; IM, intensively used meadow

was temporarily reversed due to additional irrigation according to the climate treatment. Further, land use affected soil moisture ($p < .05$), with a lower soil moisture in the intensively managed meadows. This effect was strongest in autumn (Figure S3b, land use × sampling date interaction: $p < .05$). There were no significant interacting effects between climate and land use ($p > .05$). Soil pH was not affected by any of the experimental treatments (all $p > .05$; see Figure S4).

4 | DISCUSSION

The main objective of this study was to investigate earthworm community activity responses to climate change and if these responses are modulated by different land-use types and seasons. According to our expectations, the abundance and biomass of active earthworms varied substantially across seasons and were lowest in early summer (June) when soil conditions were dry. A decrease in earthworm abundances during the summer months due to drier soil conditions has been shown in other studies (e.g., Morales et al., 2013; Walsh & Johnson-Maynard, 2016). Generally, soil moisture is a major factor determining soil biological activity (Thakur et al., 2018) as many soil organisms, including earthworms, depend critically on water availability in the soil (Coleman, Callaham, & Crossley Jr, 2017; Tondoh, Guei, Csuzdi, & Okoth, 2011; Singh et al., 2019). In our study, this was not only reflected by the

seasonal changes in earthworm abundances but also by the effects of the climate change treatment, with the lowest abundance of active adult earthworms occurring under the driest conditions (future climate in summer).

The effects of climate treatment were rather scarce in our experiment and our main hypothesis of interacting effects of climate and land use was only supported by some of the earthworm community variables. Nevertheless, abundance of active adult earthworms was significantly positively affected by future climate in spring (under wetter and warmer conditions in this treatment), but had a detrimental effect in summer and autumn. The increase in density during more moist soil conditions in spring may indicate certain activity and reproductive peaks, given that earthworms accomplish most of their life cycle during moist periods (Jiménez et al., 1998). Particularly dry conditions in the future climate treatment in summer have recently been shown to have strong negative effects on soil biological activity (Siebert et al., 2019a), and moisture conditions in autumn cannot compensate for such detrimental effects (Siebert et al. 2019b). This pattern was also reflected in the abundance of adult earthworms. Moreover, the lower abundance of adult earthworms in the intensively used meadows in summer and autumn can be related to lower soil moisture in this grassland type during that time of the year (Figure S3). The lower soil moisture in the intensively used meadow is due to the higher standing plant biomass in this treatment (mean yield in August: 12.7 dt ha dry weight) than in the extensively used meadows (mean yield in August: 7.3 dt ha dry weight). The projected extended and more severe dry periods during summer months are likely to cause a decrease in the density of earthworms in the future (Eisenhauer et al., 2014). Thus, our results support the observation of altered activity patterns of soil organisms (Siebert et al., 2019a), with unknown consequences for ecosystem functions (Eisenhauer et al., 2018) that earthworms co-determine.

Earthworm communities were significantly impacted by the different grassland types, with lowest earthworm abundance and biomass in the low-plant diversity, intensively used grassland. In addition to the effects of soil moisture discussed above, these differences among land-use types could be due to a number of non-mutually exclusive mechanisms. First, differences can be related to the plant species and functional group composition in the different grassland types. For instance, grasses are well known for their relatively nitrogen (N)-poor tissue that only sustains low earthworm populations (e.g., Eisenhauer et al., 2009; Milcu, Partsch, Scherber, Weisser, & Scheu, 2008; Spehn, Joshi, Schmid, Alphei, & Korner, 2000), especially in communities dominated by slow-growing grasses (Piotrowska, Connolly, Finn, Black, & Bolger, 2013). Legumes, by contrast, have been shown to increase earthworm populations, because of their N-rich tissue (Curry, Doherty, Purvis, & Schmidt, 2008; Eisenhauer et al., 2009; Milcu et al., 2008; Spehn et al., 2000). Earthworms as detritivores require food with a relatively high N content; therefore, they may prefer plant residues with a low C:N ratio. Legumes were absent from the intensively used managed meadows in our study, which might explain the low earthworm abundances and earthworm biomasses (also mean individual biomass). Second, higher plant diversity has been reported to have beneficial effects on soil organisms by providing a higher diversity of substrates (e.g., Eisenhauer et al., 2013; Hooper et al., 2000; Scherber et al., 2010). In the present study, plant diversity was substantially higher in the extensively used grassland types compared to the intensively used grassland (Schädler et al., 2019; Siebert, Thakur, et al., 2019). Moreover, whereas the extensively used grassland consists of three plant functional groups, the intensively used grassland consists nearly exclusively of grasses (Schädler et al., 2019). Third, N inputs by faecal matter of sheep during grazing may drive high earthworm abundance and diversity in pastures (Rutgers et al., 2016). Fourth, management treatments such as frequent harvests and input of mineral fertilizers may have detrimental effects on earthworm communities (e.g., due to a reduction of soil pH) (Coleman & Jr Crossley, 2004). However, we could not demonstrate any differences of soil pH depending on grassland type in our study (Figure S4). We therefore conclude that the effects of grassland type are mainly mediated by vegetation biomass-dependent changes in soil moisture, whereas possible further positive effects of plant diversity and dung deposition in the extensively used grasslands can be suggested.

In the present study, endogeic species were dominant in terms of total abundance and biomass, with four out of five species belonging to this group. This corresponds with the common finding that endogeic earthworms are usually dominant in grasslands (Brussaard, de Ruiter, & Brown, 2007; Didden, 2001).Species-specific abundances showed no significant influence of climate treatment and land use, but all species showed low abundances in summer. We did not observe any further consistent effects of the experimental treatments on species-specific biomasses across all endogeic species and also the anecic *L. terrestris*, indicating idiosyncratic responses of the different earthworm species. However, because earthworm species richness is usually low in agricultural sites and different species also prefer different habitats (e.g., epigeic earthworms), reliable statements regarding earthworm responses to climate and land-use change would have to be based on a more comprehensive research approach and future syntheses across studies.

In this study, no evidence was observed for the hypothesis that extensive land use can mitigate detrimental climate-change effects in comparison to intensive land use. This is in line with a recent study on soil biological activity at the same field site that observed detrimental effects of the future climate treatment irrespective of the land-use type (Siebert et al., 2019b). The authors concluded that extensively used grassland does indeed support higher levels of soil biological activity, but that new management approaches might be needed to attenuate the consequences of climate change. In this study, moreover, effects of climate treatment were clearly overruled by seasonal effects and showed rather species-specific and season-dependent ways, indicating that it could be difficult to accurately predict changes. It might be speculated that the slight tendency toward negative effects of future climate on active earthworm populations may seriously impact earthworm communities in the long run. In contrast, the detrimental effects of intensive grassland use could be demonstrated much more clearly in our study, but even here seasonal changes superimposed upon these effects.

5 | CONCLUSIONS

There is increasing awareness of the important role of interactive effects of global change factors on soil communities and processes in grasslands and other agroecosystems. Our study indicates that grassland management type affects earthworm communities and their activities, and that these effects are often mediated by the season and respective environmental conditions, whereas the effects of climate were often negligible and clearly overruled by seasonal trends. In general, the drier conditions in summer led to lower abundance and biomass of active earthworms; this effect was amplified by future climatic conditions with reduced summer precipitation. The negative effects of more intensive grassland management were most likely due to the composition and low diversity of the plant communities as well as the input of mineral fertilizers, whereas grazing may favour earthworms due to dung deposition. However, climate and grassland management showed hardly any interacting effects. These results indicate complex shifts in activity periods of soil animals in response to climate change with unknown consequences for long-term population dynamics and crucial ecosystem functions. Moreover, this study shows that considering multiple land-use types is critical for observing these important context dependencies.

ACKNOWLEDGEMENTS

JS thanks the Alexander von Humboldt Foundation, Germany, for providing financial assistance for doing research work in the Department of Community Ecology, Helmholtz-Centre for Environmental Research-UFZ, Halle, and German Center for Integrative Biodiversity Research (iDiv), Leipzig, Germany. EKC acknowledges funding from the Academy of Finland (285882) and the Natural Sciences and Engineering Research Council of Canada (postdoctoral fellowship and RGPIN-2019-05758). We appreciate the Helmholtz Association, the Federal Ministry of Education and Research, the State Ministry of Science and Economy of Saxony-Anhalt and the State Ministry for Higher Education, Research and the Arts Saxony for funding the Global Change Experimental Facility (GCEF) project. We thank the staff of the Bad Lauchstädt Experimental Research Station (especially Ines Merbach and Konrad Kirsch) for their work in maintaining the plots and infrastructures of the GCEF, and Harald Auge, François Buscot and Stefan Klotz for their role in setting up the GCEF. Further support came from the German Centre for Integrative Biodiversity Research Halle–Jena–Leipzig, funded by the German Research Foundation (FZT 118). Moreover, we thank two anonymous reviewers for their helpful comments.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

Study concept and design: NE and MS. Soil analyses: TR. Analysis and interpretation of data: JS, MS and EC. Drafting of the manuscript: JS and EC. Critical revision of the manuscript for important intellectual content: NE, EC and MS. Statistical analysis: MS. Obtained funding: JS, NE and MS. Study supervision: MS. All authors read and approved the final manuscript.

DATA AVAILABILITY STATEMENT

n/a Research data are not shared.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Singh J, Cameron E, Reitz T, Schädler M, Eisenhauer N. Grassland management effects on earthworm communities under ambient and future climatic conditions. *Eur J Soil Sci*. 2021;72:343–355. https://doi.org/10.1111/ejss.12942